

PAGEA STURROCKI GEN. ET SP. NOV., A NEW EURYPTERID FROM THE OLD RED SANDSTONE OF SCOTLAND

by C. D. WATERSTON

ABSTRACT. *Pagea sturrocki* gen. et sp. nov., a new stylonurid eurypterid from the Lower Old Red Sandstone of Angus, is described. The genus is characterized by the possession of ctenopterid-type prosomal appendages, but other features of the prosoma resemble those of *Stylonurus* s.s. The affinities of the new genus are fully discussed and its anatomy compared with that of other stylonurid genera. Finer characters of the anatomy of the prosoma and prosomal appendages of Scottish type material of *Stylonurus* s.s. and *Ctenopterus* are described for the first time.

AMONG a collection of Old Red Sandstone fossils, generously presented to the Royal Scottish Museum by the Dundee Naturalists' Society, there is a magnificent stylonurid eurypterid, in a remarkably good state of preservation, which is the subject of the present paper. Unfortunately the circumstances under which this specimen was acquired by the Dundee Naturalists' Society are not known and so its provenance is incomplete. It is clear, however, that the large flagstone block, in which the specimen is preserved, was derived from the Lower Old Red Sandstone of Angus, and the lithology and mode of preservation would suggest that it comes from one of the quarries in the Carmyllie Group (Hickling 1908). Before reaching the museum the specimen had been rather ill-advisedly 'developed' as a result of which details of parts of the prosoma and prosomal appendages have been lost. It is probable that the left extremities of the body segments, together with most of the fifth and sixth prosomal appendages of the left side, were lost with the counterpart which has not been traced. With these exceptions, however, the specimen presents us with one of the most complete and one of the largest members of the Stylonuridae, and a notable addition to the fauna of the Scottish Old Red Sandstone.

Many years have passed since the classic descriptions of Scottish stylonurid material were made by David Page (1856*a, b*, 1859), Henry Woodward (1864, 1865*a, b*, 1866-78), and Malcolm Laurie (1892, 1893, 1899). Occasion is taken in the present paper, therefore, to redescribe and refigure certain details of the anatomy of *Stylonurus* s.s. and *Ctenopterus* made possible by a re-examination of the type material in the light of more recent work by European and American authors. This was a necessary study before affinities of the new genus could be properly determined.

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SYSTEMATIC DESCRIPTION

Genus *Pagea* nov.

Diagnosis. Large stylonurid eurypterid. Third and fourth prosomal appendages bearing a double row of numerous flat spines, fifth and sixth prosomal appendages simple, keeled, tapering; sixth appendage reaching as far as the pretelson. Shape of prosoma probably subrectangular, lateral eyes in the anterior half of the prosoma, subcentral.

Ventral marginal rim of prosomal doublure broad, crossed anterior to the lateral eyes by the epistomal sutures which converge posteriorly between the eyes; breadth of epistomal plate greater than its length, transverse line of doublure parallel with anterior margin of prosoma. Anterior margin of prosoma straight, uncrenulated. Metastoma narrow in relation to the width of the prosoma, its length being over twice its breadth, anterior notch fairly shallow. Abdomen slender with lateral epimers on the post-abdominal segments, axial furrows present on all abdominal segments. Telson long, styliform, keeled.

Genotype. *Pagea sturrocki* gen. et sp. nov.

Derevatio uominis. Named after David Page (1814-79), early worker on the Old Red Sandstone fauna of Scotland and describer of the first stylonurid.

Pagea sturrocki gen. et sp. nov.

Plate 20, figs. 1 and 2, text-figs. 1 and 2.

Diagnosis. Characters as for the genus. Pretelson greatly lengthened, being over three times as long, measured on the median-line, as the postabdominal segment immediately anterior to it.

Holotype. Royal Scottish Museum. No. 1956.14.11 from the Lower Old Red Sandstone of Angus, Scotland.

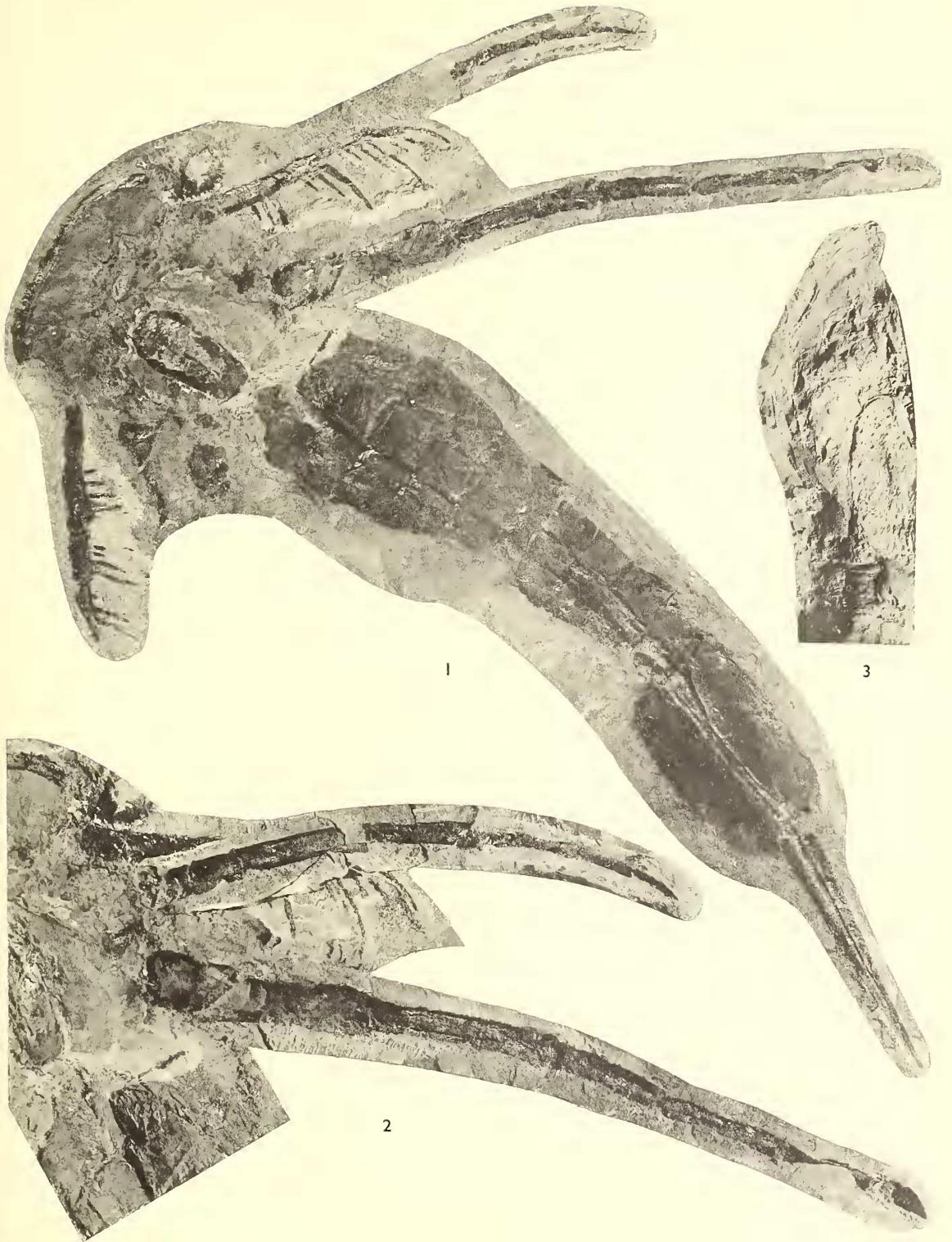
Derevatio uominis. Named after Edwin D. Sturrock, Esq., President of the Dundee Naturalists' Society, through whose generosity the holotype was acquired for the national collection.

Description of the holotype. *The prosoma.* The specimen is seen in dorsal aspect but the dorsal surface of the prosoma is not preserved, the only dorsal character which can be seen being the mounds of the palpebral lobes of the lateral eyes. These are circular and have a subcentral position but are in the anterior half of the prosoma. Each eye is slightly nearer the median axis of the specimen than to the nearest portion of the lateral margin of the prosoma. It is probable that the axes of the lateral eyes are subparallel. The anterior part of the prosomal doublure is well preserved, although the lateral portions are not present. The almost straight, undecorated, anterior edge, passing gradually into curved antero-lateral angles, suggests that the shape of the prosoma was subrectangular. There is a broad marginal rim. The epistomal sutures (r.e.s., text-fig. 1) are well preserved and define a trapezoid epistomal plate in which the greatest lateral dimension is at the anterior margin and is approximately two and a half times the length of the plate measured along the median axis. The transverse line (tr.l) of the doublure is parallel with the anterior margin. A median keel (m.k.) is present. Antelateral sutures do not appear to be present. In order to establish the characters of the metastomal plate (mts.) part of the coxa of the right sixth appendage, which obscured it, was

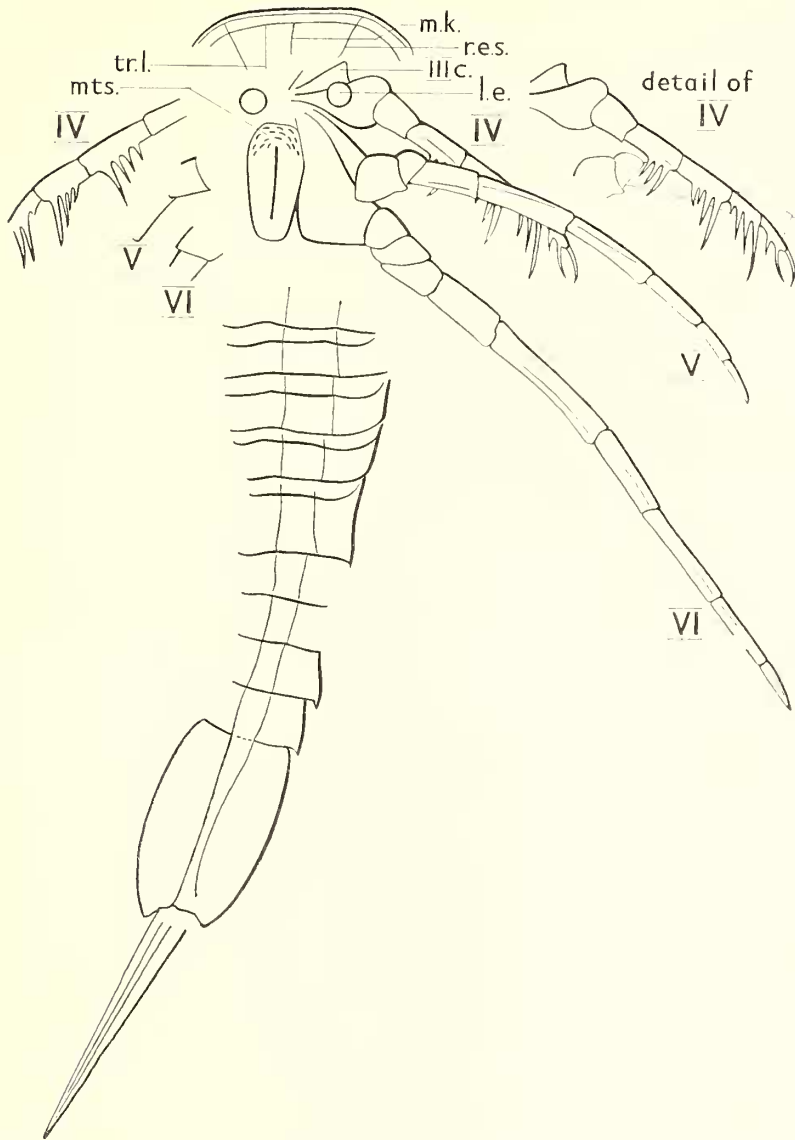
EXPLANATION OF PLATE 20

Figs. 1-2. *Pagea sturrocki* gen. et sp. nov. 1, The holotype (R.S.M. 1956.14.11), Lower Old Red Sandstone, Angus, Scotland, $\times \frac{1}{3}$, the fifth prosomal appendage having been removed to reveal the fourth appendage. 2, The right prosomal appendages of the same, $\times \frac{3}{7}$, showing the fifth appendage in position.

Fig. 3. *Ctenopterus elegans* (Laurie). The holotype (R.S.M. 1897.32.66), Gala-Tarannon, Gutterford Burn, Pentland Hills, Midlothian, $\times \frac{1}{2}$, left side of prosoma showing metastoma and prosomal doublure.



WATERSTON, *Pagea sturrocki*



TEXT-FIG. 1. *Patea sturrocki* gen. et sp. nov., drawing of the holotype (R.S.M. 1956.14.11), $\times \frac{1}{4}$.
 m.k. = median keel, r.e.s. = right epistomal suture, tr.l. = transverse line, l.e. = lateral eye, mts. =
 metastoma.

removed. The metastoma is coffin-shaped, being broadest one-quarter of its length from the anterior. The angles are rounded, and there is a shallow anterior notch. The length of the metastoma is more than twice its greatest breadth. The anterior part bears a sub-squamate pattern and a median keel extends over the central half of the plate.

The prosomal appendages. The fourth, fifth, and sixth appendages of the right side are preserved in their entirety. The fifth appendage is crossed over the fourth and part of the

former was temporarily removed to exhibit the complete fourth appendage at a lower level in the matrix. The coxa of the third and part of the coxa of the second appendages of the right side are also seen. There has been some displacement between the coxae of the fourth and fifth appendages. On the left side four joints of the fourth appendage are present but parts of two joints only of the fifth and sixth appendages are seen. The fifth prosomal appendage is 1.7 times the length of the fourth, and the sixth is 1.3 times the length of the fifth. The fourth appendage has six joints as well as the coxa, the proximal five of which bear spines. The spines on the second, third, and fourth joints are borne in two rows of four spines, the length of the spines increasing towards the distal end of each joint. The longest spines of each joint increase in length from second to third and from third to fourth joint. The spines are flat and striated. The penultimate joint bears fewer spines than the joints proximal to it and the ultimate joint of the fourth appendage appears to take the form of a spine of similar type to those borne on the other joints. The fifth prosomal appendage is composed of eight joints due to the presence of a double trochanter. This appendage does not bear spines but is keeled and tapers distally. The sixth appendage is similar to the fifth, being free of spines, keeled, and tapering distally. It is unusual, however, in being composed of nine joints, there being a double trochanter and an extra joint between the trochanter and the pre-femur. The sixth appendage reaches posteriorly to the level of the pretelson.

The abdomen. The posterior five pre-abdominal tergites are seen in dorsal view, the first two not having been preserved. In the case of four of the tergites the doublures are well seen. The right lateral margins of the posterior three tergites are the only ones preserved, all the other margins having been lost through breakage. Such evidence as is provided by the margins present, however, would suggest that the posterior part of the pre-abdomen gradually tapers posteriorly. The segments are relatively narrow compared to their length. The posterior pre-abdominal segment appears to be longer than the others, and its post-lateral angles are produced into an acute form if not quite an epimer. The pre-abdominal segments bear distinct axial furrows dividing the tergites into axial and pleural portions. The axial furrows are placed slightly closer together as tergite succeeds tergite posteriorly. The reconstruction (text-fig. 2a) shows a simple axial portion of the pre-abdomen. It is possible, however, that the axis may have been formed of two lobes divided by a median furrow and that none of the left pleural parts of the tergites remain on the holotype. If this were the case, the reconstructed width of the pre-abdominal tergites would be increased by approximately one-third over that shown in the text-figure. Ventral structures of the abdomen are not seen, thus the nature of the operculum and median abdominal appendage remains unknown.

All five postabdominal segments are preserved, but the margins of the fifth only are complete. The right margins of the third and fourth are present but other margins are lost due to breakage. From the evidence of the third and fourth postabdominal segments it is clear that the first four segments of the postabdomen bore small epimerae. Like the pre-abdominal segments they are narrow in comparison with their length. The pretelson is remarkably specialized. It is between three and four times the length of the other postabdominal segments and has a barrel-shaped outline, the lateral margins being regularly curved and the greatest width of the segment being midway along its length. Posteriorly the curves of the margins converge without interruption to form the

outer margins of the broad epimeral angles. As with the pre-abdominal tergites, the postabdominal segments bear axial furrows which, on the first four segments, converge slightly posteriorly, from segment to segment. On the pretelson, however, the axial portion is waisted and the pleural parts barrel-shaped, the axial furrows curving regularly in the opposite sense to the margins of the segment. The entire abdomen is ornamented with a fine granulation.

The telson is long and styliform. The axial ridge is continued on the telson, the furrows being straight and converging posteriorly to meet at the posterior tip of the telson. The ridge has more the nature of a keel in its posterior third.

Measurements of the holotype. Probable length of prosoma 120 mm., probable breadth of prosoma 120 mm. Length of metastoma 62 mm., maximum breadth of metastoma 31 mm. Distance from anterior margin to lateral eyes 43 mm., distance between lateral eyes 33 mm. Greatest distance between epistomal sutures 70 mm.

Measurements of fourth prosomal appendage: trochanter 22 mm.; femur 32 mm.; patella 32 mm.; tibia 22 mm.; tarsus 20 mm.; pretarsus 20 mm.

Measurements of fifth prosomal appendage: trochanter 1, 23 mm.; trochanter 2, 11 mm.; prefemur 32 mm.; femur 53 mm.; patella 51 mm.; tibia 37 mm.; tarsus 25 mm.; pretarsus 25 mm.

Measurements of sixth prosomal appendage: trochanter 1, 17 mm.; trochanter 2, 15 mm.; prefemur 1, 17 mm.; prefemur 2, 41 mm.; femur 77 mm.; patella 48 mm.; tibia 57 mm.; tarsus 42 mm.; pretarsus 28 mm.

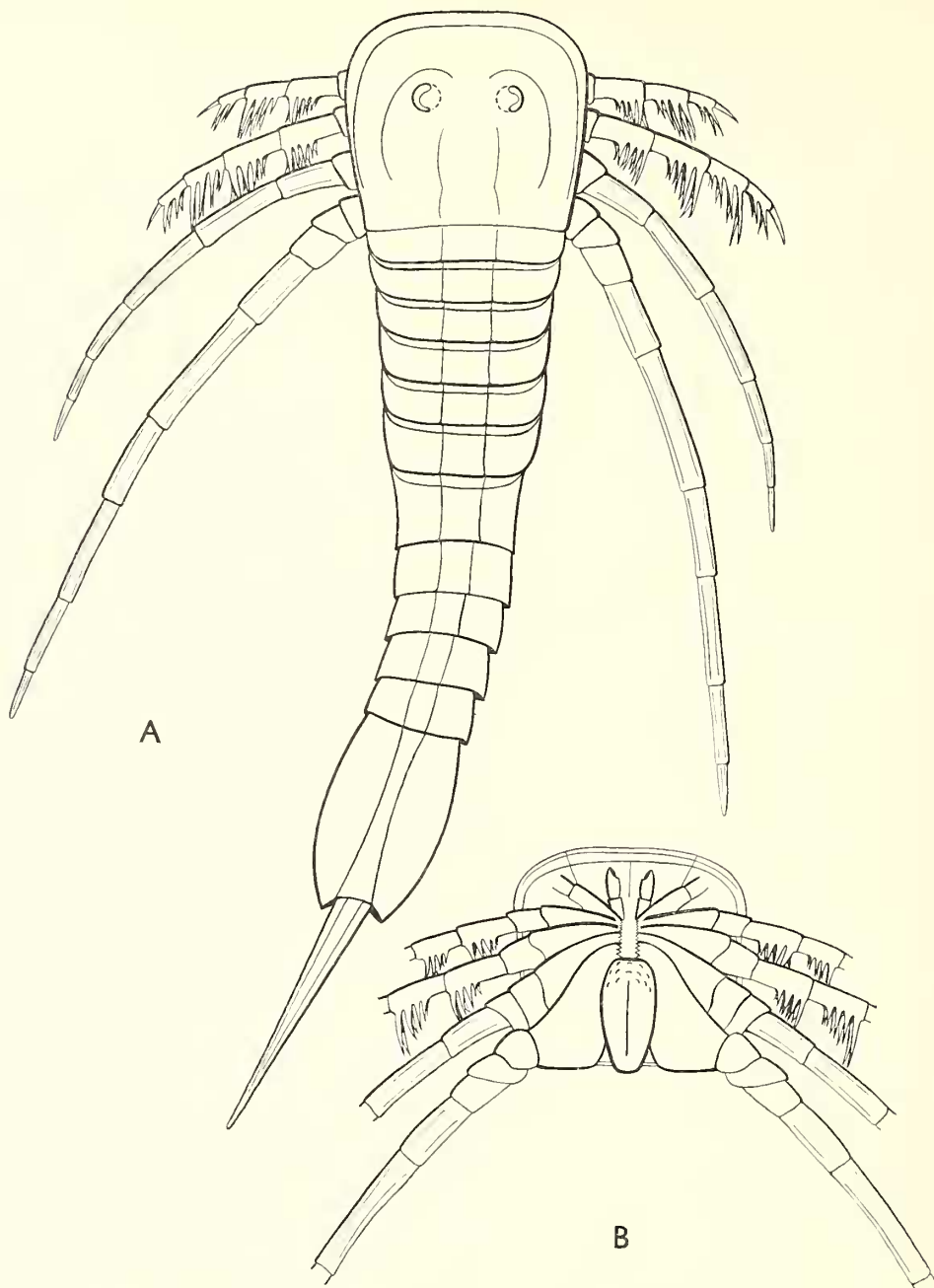
Measurements of the pre-abdomen: 7th and 8th segments not known. 9th, length 25 mm.; 10th, length 25 mm.; 11th, length 29 mm., restored maximum breadth based on measurement of complete right side of tergite 84 mm.; 12th, length 27 mm., restored maximum breadth 80 mm.; 13th, length 39 mm., restored maximum breadth 66 mm.

Measurements of the postabdomen: 14th, length 24 mm.; 15th, length 25 mm.; 16th, length 27 mm., restored maximum breadth 60 mm.; 17th, length 27 mm., restored maximum breadth 56 mm. Length of pretelson 97 mm., maximum breadth 65 mm. Length of telson 141 mm.

The restoration (text-fig. 2a and b) follows directly from the observed characters of the holotype (text-fig. 1) except for the form of the prosoma, the nature of the chelicerae, and the third prosomal appendage. Because of the similarity of the observed anterior portion of the prosoma to that of *Stylonurus powriei* Page, and because the form of the prosoma in *S. powriei* appears to agree with that suggested by the ventral configuration of *P. sturrocki*, a prosomal outline closely approximating to that of the Scottish Lower Old Red Sandstone form *S. powriei* has been adopted in the restoration. The third prosomal appendage has been drawn like the observed fourth appendage since the three posterior walking legs of the new eurypterid closely resemble those of *Ctenopterus*, a genus to which it appears to be related, and it is assumed that, as in *Ctenopterus*, the third and fourth prosomal appendages would be similarly spinose. The chelicerae (text-fig. 2b) have been reconstructed as fairly broad, a character which appears to be common to stylonurid eurypterids and described in such forms as *Ctenopterus excelsior* (Hall) (in Hall and Clarke 1888) and *Brachyopterus pentagonalis* (Størmer) (in Størmer 1934).

AFFINITIES

The morphological features of *Pagea sturrocki* make it clear that the new Scottish eurypterid is a member of the Family Stylonuridae of Diener 1924 as emended by Størmer (1951, p. 413). It shows a curious mixture of characters usually associated with the genera *Stylonurus* s.s. and *Ctenopterus* in addition to which there are features, such



TEXT-FIG. 2. *Pagea sturrocki* gen. et sp. nov., diagrammatic reconstructions. A, Dorsal view, $\times \frac{1}{4}$,
 B, Ventral view of the prosoma and proximal portions of the prosomal appendages, $\times \frac{1}{4}$.

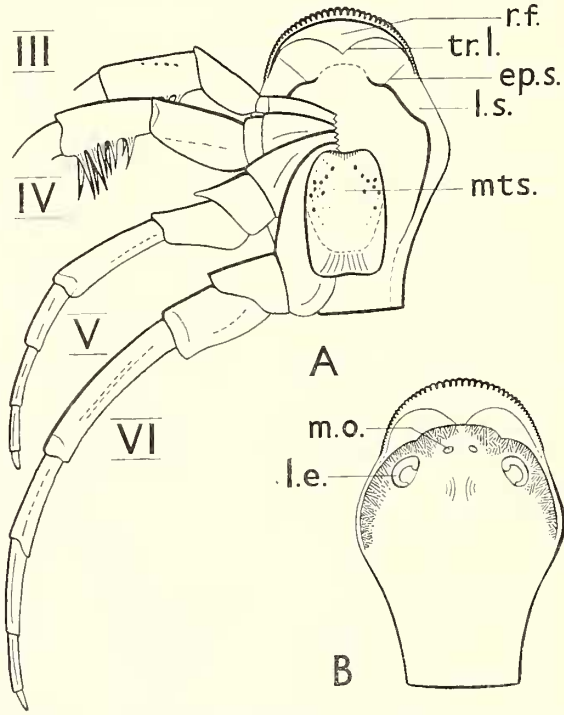
as the marked trilobation of the abdomen and the extraordinary enlargement of the pretelson which are specializations not seen to the same degree in either of these genera.

Affinities with Ctenopterus Clarke and Ruedemann 1912. The prosomal appendages of *Pagea sturrocki* are similar to those of *Ctenopterus* in having a double row of flat spines on the fourth, and presumably the third, appendages while the fifth and sixth are long, keeled, and without spines. The best-known species of *Ctenopterus* is the genotype *C. cestrotus* (Clarke) from the Shawangunk Grit, Middle Silurian, of Otisville, New York State. The joints of the third and fourth appendage of this species bear between six and nine pairs of spines which are of approximately equal length. Clarke was able to develop the underside of one of the two known specimens of *C. excelsior* (Hall) from the Catskill Group, to reveal the chelicera and second appendage of the prosoma which bore paired spines, but, as noted by Clarke and Ruedemann (1912, p. 292), in Beecher's famous restoration of this gigantic eurypterid (1900, pl. 1), as in their own restoration of it (1912, pl. 47), the paired spines shown on the third and fourth appendages were restored after *C. cestrotus* and have never been seen in *C. excelsior*. It is in the Scottish species *C. elegans* (Laurie) from the Gala-Tarannon Beds of the Pentland Hills, however, that the appendages of *P. sturrocki* can be most closely matched. Although the increase in the size of the spines distally on each joint, shown by *Pagea*, is not so well seen in *C. elegans*, the spines on the distal joints of the third and fourth appendages of that species certainly do show an increase in size as in *Pagea*. The spines are also similarly striated.

While the appendages of *P. sturrocki* are similar to those of *Ctenopterus*, the prosomal characters differ. In *Pagea* the axes of the lateral eyes appear to be almost parallel, in contrast to the axes in *Ctenopterus* which converge anteriorly. The shape of the prosoma in *Ctenopterus*, where it is known, as in *C. cestrotus*, *C. elegans*, and *C. excelsior*, narrows anteriorly, the greatest width being in the posterior half. Unlike the strongly curved anterior margin of *Ctenopterus*, *Pagea* has an almost straight anterior margin. In dealing with the restoration of *Pagea*, reasons have been given for supposing that the shape of the prosoma was probably similar to that of *S. powriei*. Although likely, however, this cannot be proved until more specimens come to hand, but a comparison of the prosomal doublures in *Pagea* and *Ctenopterus* reveals a distinction. Clarke and Ruedemann (1912, p. 289) state that the prosomal doublure (= ventral marginal rim, see Størmer 1934, p. 22) of *C. cestrotus* is broad and thick and widest along the frontal margin where it exhibits a deep concentric furrow. An unsatisfactory picture is given (pl. 49, fig. 2) in illustration of this description. In the original illustration of *C. excelsior* (Hall 1888, pl. 26) one of the epistomal sutures is indicated. Otherwise the nature of the ctenopterid doublure appears to be unknown. Re-examination of the type material of *C. elegans* (Laurie), a species which Clarke and Ruedemann regarded as typical of their genus *Ctenopterus*, has provided further evidence of the ventral structures of the prosoma of that genus.

Laurie's description of *Ctenopterus elegans* (1899, p. 580) was based on five specimens which he regarded with certainty as belonging to this species. Of these, two appear to be the right and left sides of the same specimen and are now mounted together (R.S.M. 1897.32.66) and were figured by Laurie as figures 13 and 19. A third (R.S.M. 1897.32.190) was figured (fig. 14) and shows the dorsal aspect of the anterior part of the prosoma and clearly demonstrates the convergence of the margins of the prosoma towards the anterior.

The other two specimens used by Laurie, but not figured by him, are R.S.M. 1897.32.67 and 1897.32.66A. Re-examination of the figured specimens has made possible a restoration of the prosoma in ventral and dorsal aspect (text-fig. 3a and b). In the restoration the shape of the prosoma has been taken from 1897.32.66, the largest specimen, in which the outline is preserved on the left half where the margin is complete except for a portion at the median part of the anterior. This part was restored from 1897.32.190 in which the anterior is complete. The dorsal structures are drawn from 1897.32.190, but



TEXT-FIG. 3. *Ctenopterus elegans* (Laurie), diagrammatic reconstructions based on the holotype (R.S.M. 1897.32.66), also R.S.M. 1897.32.190, both from the Gala-Tarannon of the Gutterford Burn, Pentland Hills, Midlothian. A, Ventral view of the prosoma and prosomal appendages of the right side, showing form of the prosomal doublure and metastoma, $\times \frac{1}{3}$. B, Dorsal view of the prosoma, $\times \frac{1}{3}$. r.f. = rostral field, tr.l. = transverse line, ep.s. = epistomal suture, l.s. = lateral shield of doublure, mts. = metastoma, m.o. = median ocella, l.e. = lateral eye.

the position of the lateral eyes is also seen in 1897.32.66 from which the ventral structures were drawn. The prosomal doublure is well shown in 1897.32.66 in which part of the left half of the epistoma, the left epistomal suture and the left lateral shield are preserved. The doublure is deep anteriorly, restoration indicating that the epistoma, at its greatest width, is approximately twice as broad as it is long, measured in the median line. The greatest width of the plate lies approximately at the mid point. The epistoma is crossed by an arcuate transverse line defining a rather large rostral field. The absence of the median part of the anterior of the specimen makes it impossible to say whether or not a median keel is present. A crenulated border is present which is deepest anteriorly and

narrows laterally. The lateral shields of the doublure are narrow, the inner margins tending to follow the outline of the prosoma, but converging towards it posteriorly. No antelateral suture is indicated.

The characters of the prosomal doublure as shown by *C. elegans* differ markedly from those of *Pagea sturrocki*. The difference in the outline of the prosoma is reflected in a different shape of epistomal plate which in *Pagea* is relatively broader than in *Ctenopterus* with the maximum width at the anterior margin of the plate instead of at the mid point. The transverse line in *Pagea* is simple instead of arcuate as in *Ctenopterus elegans* and the rostral field much less large.

From the left side of R.S.M. 1897.32.66 it is clear that the metastoma of *Ctenopterus* is broad in relation to its length and also in relation to the width of the prosoma. The plate is subrectangular in shape, the length being only about one and a half times the greatest breadth. There is a shallow anterior furrow which is ornamented at the margin by small crenulations. The antero-lateral areas of the plate are ornamented with pustules of various sizes. At the posterior and postero-lateral parts of the plate there is an area of centrally directed anastomosing ridges, the ridges terminating at the margins of the plate, and anteriorly along a curved line extending from the margins of the plate about the middle of its length posteriorly to cross the median axis one-fifth of the length of the plate from the posterior margin. The indentation of the margin at the left postero-lateral angle shown by Laurie (1899, fig. 13) does not exist and was due to the matrix hiding the form of the plate at this point. Development of the plate reveals the shape as that shown in text-fig. 3a.

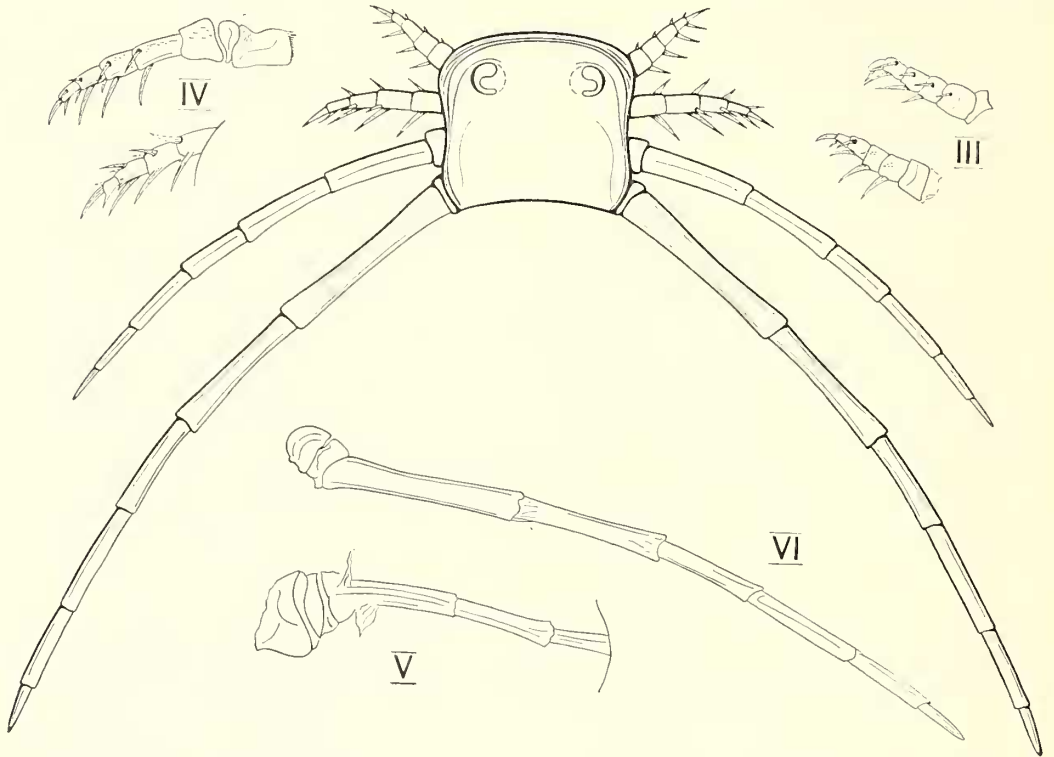
The form of the metastoma in *Ctenopterus elegans* is therefore quite distinct from that of *Pagea* in shape, in the greater relative breadth, and in the high degree of ornamentation.

Affinities with Stylonurus Page 1856. It is unfortunate that the only specimen of the genotype *Stylonurus powriei* Page (R.S.M. 1891.92.101) shows only the fifth and sixth prosomal appendages, the anterior appendages not having been preserved. The discovery of *Pagea* gives rise to an interesting speculation with regard to this specimen since it now appears quite possible that had the third and fourth appendages been preserved they need not have been simple as in *S. logani*, but could have been spinose as in *Pagea* since other characters of the body, such as the shape of the prosoma and the slight trilobation of the abdomen, are similar to the new genus.

Where the prosomal appendages of *Stylonurus* species are better known, as in *S. dolichopteroïdes* Størmø (1934, p. 103), *S. macrophthalmus* Laurie (1899, p. 579), and *S. ornatus* Laurie (Lamont 1955, p. 211), it is clear that they form a graded series increasing in length posteriorly, the first three pairs of walking legs bearing spines and the last two being free of spines. Since the publication of Woodward's reconstruction of *S. logani* (1866-78, text-fig. 131) there has been some doubt as to whether the appendages of this species conform to the general stylonurid pattern, and later authors such as Clarke and Ruedemann (1912, pp. 278-84) have made it clear that they regarded Woodward's reconstruction, with the subequal third and fourth appendages and the much longer but subequal fifth and sixth appendages, as being in error. Since *S. logani* was one of the forms which was illustrated by Page in his first figures of the genus (1859, p. 181, fig. 1) the present opportunity is taken to correct Woodward's reconstruction

and confirm that the appendages of this species do conform to the general stylonurid pattern.

S. logani is known from the holotype only of which the part is in the Geological Survey Museum (GSM. 87357) and the counterpart in the Royal Scottish Museum (1891.92.33). Although the Survey specimen was figured by Woodward in his monograph (1866-78, pl. xxiv, fig. 1) it was the counterpart that he figured in his original



TEXT-FIG. 4. *Stylonurus logani* Woodward, diagrammatic reconstruction of the holotype, based on the counterpart (R.S.M. 1891.92.33), dorsal view of prosoma and prosomal appendages, $\times 1$, with drawings of the prosomal appendages as they appear on the counterpart, $\times 1\frac{1}{2}$ approx.

description (1864, pl. x, fig. 1) and this specimen bears more evidence of the prosomal appendages, which in most cases have become detached from the body, than does the Survey specimen. A re-examination of the counterpart has made possible the reconstruction in dorsal aspect reproduced in text-fig. 4. This was done by making careful drawings of the legs as they appear on the specimen (text-fig. 4, III-VI) and reassembling them with the prosoma in restoration in dorsal aspect. The visual areas of the palpebral lobes of the lateral eyes are also seen clearly in this specimen and have been drawn in the reconstruction.

There is no serious exception to the generally accepted pattern of the prosomal appendages of *Stylonurus* s.s., but it is clear also that the appendages of *Pagea*, with their many pairs of flat spines on the joints of the third and fourth appendages, are